

defined, canalicular system, as one of Dr. J. E. Gray's family of Clioniadae.

The yellow colour and dimpled appearance, respectively, presented by the coriaceous envelope of the gemmule is owing to its being composed of minute spherical cellules, about 1-3700th of an inch in diameter, situated about the same distance from each other, but united together, in a stellate form, by intervening straight tubules, five or six in number, radiating from each cellule, similar to what is seen in the microscopic cell-structure of fossil Foraminifera, ex. gr. *Orbitoides*; and it is in the intervals between the cellules and radii that the dimples occur.

XI.—*Reply to Mr. Frederick Smith on the Relations between Wasps and Rhipiphori.* By ANDREW MURRAY, F.L.S.

I was much pleased to read my friend Mr. Frederick Smith's commentary on my paper about Wasps and *Rhipiphori* in the last Number of the 'Annals,' although I see that I have not succeeded in converting him to my views. There is nothing like the collision of opposing minds for eliciting truth; and it is always pleasant to find another taking interest in a subject which has excited our own, especially when it is so fairly and honestly handled as every subject is on which Mr. Smith expresses his opinion.

With the help of that fairness, I do not yet despair of bringing him round; and for that purpose, as well as for the sake of those who may have been convinced by his arguments or led away by the authority of his opinion on a subject on which he is *facile princeps*, I shall ask him and them again to weigh the difficulties which his view of the question presents. In my last paper I was more concerned in stating my own observations than in controverting the opinions of others; but I shall now pass in review the whole facts that we know on the subject, either from Mr. Smith, Mr. Stone, myself, or others, and endeavour to see with which explanation they best agree.

Mr. Smith agrees with me that the *Rhipiphorus* lays its eggs in the cells of the wasps, and that in the instances in which I saw two eggs in one cell, one of them must have been a *Rhipiphorus*; that gives us the form of its egg and its position and mode of attachment in the cell (which are all identical with those of the wasp's). When the wasp's egg is examined in its early stage, it is seen to be simply an oval egg, with a smooth semitranslucent shell, through which, at a later

period, the form of the larva can be distinguished, when viewed as a transparent object. It is fixed, by the narrow end, in an angle of the cell about a third of the way from its base. By-and-by it looks as if it had a head, and by-and-by like a larva holding on by the tail. How it comes out of the shell, or whether it ever comes out of the shell, I do not know; most likely Mr. Smith can say. It may be that the egg-shell is absorbed and becomes practically the first skin of the larva. Looked at later, or, I should rather say, in a further advanced specimen (for that is the way in which the changes practically are observed), we find the larva nearer the base of the cell: it is travelling to the bottom. It cannot fall out of the egg-shell to reach it at one stroke; for the cell is mouth down and the bottom is at the top: it cannot fall up; it therefore has to work upwards. How it does so, is, I think, not known. It is said by some to be by throwing itself into a loop and catching hold of the wall of the cell with its teeth, then releasing the tail and throwing another loop, fastening its tail again as a sucker and releasing its head, and so on, by a succession of slow summersaults; but this to me seems impossible. At the stage in question it is a dumpy fat oval thing which, to all appearance, could no more bend itself into a loop than a hogshead could. But be that as it may, somehow or other the young larva manages to wriggle itself (perhaps by slow action of its sucker tail) up to the bottom of the cell. Now the first question I should like to ask Mr. Smith is, whether this helpless larva is fed by the parent wasps before it reaches its goal, the bottom of the cell, or not. I see no reason why it should not, but almost a necessity that it should. The journey to it, especially if made by the process of shifting its sucker tail without letting go its hold, must not only be a slow one, but one involving considerable exertion. We all know (that is, all entomologists know) how soon a larva freshly excluded from the egg shrivels up if its food is not at its mouth the moment it comes out, and we are never tired of admiring the wonderful precautions which the parent insect takes to ensure that its offspring shall find itself in the midst of plenty from the very first. I therefore believe that it *is* fed, and fed with soft food fitted for its tender jaws.

But how about the young *Rhipiphorus*-larva? Is it fed too? And here it is scarcely a digression (certainly not an irrelevant one) to ask what the larva is like. So far as I know, it has never been properly described or figured. Candèze and Chapuis, in their works on the larvæ of Coleoptera, give no description; they refer to a notice of it by Ramdohr in Germar's *Mag. für Entom.* i. (1813) p. 137, but which is without de-

scription. Neither does Westwood give or refer to any description in his great work; and I can find none anywhere else. Mr. Stone is the first who gives some details about it: his description is as follows:—

“The larva is a singular-looking one. The head is bent forward under the body; between the segments it is more deeply furrowed than any larva with which I am acquainted. A longitudinal furrow extends down the back from the head to the anal extremity, cutting each segment across. The skin, during life, throughout the whole of the course of this furrow, is perfectly transparent, so that the workings of the internal organs may be plainly seen. The body of the larva, while alive, has the appearance of a thin transparent skin filled with minute particles of curd. These appearances vanish after death, when the body becomes dense and has an appearance of solidity about it which it had not before.” (Stone in ‘Zoologist,’ 1865, xxiii. p. 9462.)

But this description is obviously imperfect. He does not tell us whether it has feet or not—a not unimportant point when the question is whether the larva passes a nearly motionless life in one cell, or a roving one, preying upon grubs in other cells. But the context implies that it is like the grub of the wasp, and consequently apodal; and Mr. Smith informs me that it is so. I remember perfectly, in my examination of the wasps’ nest out of which this question has arisen, seeing plenty of grubs with the back so transparent as to show the inside like curds shining through. If these were the larvæ of the *Rhipiphorus*, then they are as like to the wasp-grub as one pea to another—so like, in fact, that they did not attract my attention as being distinct. Their powers of motion, then, are similar to those of the wasp; and I state it as a fact beyond contradiction that the wasp-grub *cannot* walk. When taken from its cell, it lies like a sack of meal: it may wriggle a little; but as to rising up and walking, it can no more do it than the sack can. Once fixed and hanging by the tail, all they can do seems to be to shift their position a little. But, passing that, the question I ask is, how the *Rhipiphorus*-larvæ are sustained at first until they reach their supposed prey, if not by the wasp-nurses. The journey of the young larva, according to Mr. Smith’s view, is in an opposite direction to that of the wasp’s, viz. to the mouth of the cell, to go roving about in search of a wasp-larva on which to pounce and prey; its journey is thus longer. It must be a longer time without food, and undergo greater exertion requiring food, travelling about like a Blondin on the edges of the cells—only like a Blondin upside down:

and when it gets to its food (the wasp-grub), it has a tough skin for its tender young jaws to break through before it can begin, and must encounter the risk of being first gobbled up by the big wasp-grub, whose jaws are gaping for food at the very door. It seems to me that it would be a safe speculation to lay long odds on the wasp-grub having the best of it. If Mr. Smith says it is not fed at all until it takes a wasp-grub at unawares, then I invite him to consider the difficulties attending the promenade which he supposes it to make before breaking its fast. If he admits that it must be fed by the wasps to begin with, then I ask him to say, on abstract grounds (putting Mr. Stone's observations out of view for the present), why he should object to its being fed by the wasps more at one time of its life than another.

But there are more anomalies in Mr. Smith's way than that. Suppose that it does not require to be fed, or that, if it requires to be fed, it is fed by the wasps until it reaches its victim, and that then it escapes its jaws and fastens upon it, I want Mr. Smith to say whether it feeds only upon one victim, or if, after eating it up, it comes out again, and goes roaming about from cell to cell, destroying a succession of grubs. It must do either the one or the other. Let us test both. First, that it only destroys one grub. As the *Rhipiphorus*-pupæ and perfect insects ready to come out are always found in cells closed-in by a lid which Mr. Smith maintains to be spun by the wasp-larvæ*, the *Rhipiphorus*-grub must make its lodgment in the victim's cell just before it is beginning to spin, and must make so little progress in its attack upon it at first as to leave it at least power to spin the lid. When it is spun, the two will then be shut up together, and the little tiny grub has full scope to tear away at the vitals of the wasp, probably now become a pupa. But does Mr. Smith think that a meal of one animal can suffice to nourish another into as great dimensions as the animal eaten. True, a caterpillar infested with ichneumons often nourishes within its bosom a tribe of parasites whose aggregate bulk is not much inferior to its own; but they have not had merely a mass to eat equal to its bulk; they have grown with its growth, and fresh food has been assimilated for them day by day—so that they have eaten the

* I have to acknowledge the justness of Mr. Smith's correction of a *lapsus penne* in my last paper, where I spoke of the pupæ spinning these lids, instead of the larvæ. The contrast in my line of thought was not between pupæ and larvæ, but between the lid being spun by the creature inside the cell or lid, or by the parents outside. Of course when the larva changes into a nearly motionless inactive pupa, there could be no question of spinning. The error corrected itself.

bulk of many caterpillars. With the *Rhipiphorus* there is nothing of this. The assumption is that it attacks from within. The wasp-larva or pupa has ceased to eat, or if not already ceased, the attacks of its enemy will soon make it cease; and all that the little larva of the *Rhipiphorus* has to feed upon and grow as large as the wasp upon is the one mass of meat no larger than what it is to grow to. This is the view which Mr. Stone and, following him, Mr. Smith adopt. Mr. Stone's observation is that the *Rhipiphorus*-larva which he found attacking a wasp-larva in a sealed-up cell (which, by the way, must only have been recently closed, or it would have had within it not a wasp-larva, but a wasp-pupa) "was of *minute size* when discovered, and appeared to have only recently fastened on its victim; but so voracious was its appetite, and so rapid its growth, that in the course of the following forty-eight hours it attained its full size." Now if by "*minute size*" we suppose a line or a line and a half in length, it must have grown three or four times its own size in forty-eight hours, which is so opposed to everything we know of the laws of development and assimilation that I cannot accept it. If we look at the little black deposit of digested debris at the bottom of the wasps' cells, we find fragments indicating the consumption of hundreds of insects not much smaller than themselves: there is the same at the bottom of the cells of the *Rhipiphori*; but I refrain from using that as an argument, because Mr. Smith might plead that I cannot prove that the black deposit in their cells was not the product of former wasp-tenants who had been reared in the same cell.

Let it not be supposed for a moment that I at all doubt that Mr. Stone thought he saw this; but I think his observation has been inaccurate; and I try to account for it in this way:—It is plain he could not have kept his eye constantly fixed on this specimen for forty-eight hours; we may assume that he did not sit up two nights running to watch it. He saw it attacking the wasp-larva and eating at it voraciously (the meaning of that and of some other of his observations I shall discuss presently), and he left it so occupied. He returned to it, how soon or how often he does not tell us; but when he did return, and found it so increased in bulk, I cannot but believe that he mistook the cell, and, instead of looking into the one he left, looked into another where was a mature *Rhipiphorus*-larva, which had had nothing to do with the meal on the wasp. Any one who has ever tried the experiment of endeavouring to find a particular cell in a comb after removing his eyes from it, for however brief a space, will know that nothing could be easier than to make such a mistake. I can

speak to it from experience. In placing the nest from which I took my *Rhipiphori* in the South-Kensington Museum, I thought it might be desirable to mark the cells out of which I had taken *Rhipiphori*; and I accordingly set about doing so by painting blue the lid of each cell out of which I took one. At first I attempted to do it by first taking out the insect and then painting the lid; but I found the short space of time between laying down the forceps and taking up the painting-brush sufficient to efface or render uncertain the identity of the cell from which it had been taken. I therefore had to take the precaution of painting the half-opened lid before I drew out the *Rhipiphorus*.

But, further, if the rate and mode of growth of the *Rhipiphori* is that stated, they should always be found engaged in the way Mr. Stone describes. They should always be found in sealed cells, if one wasp-grub is sufficient to nourish them; whereas this is the only instance that has ever been observed of it. (Mr. Smith says no; but I shall presently show that it is.) Mr. Stone himself records having found a number of larvæ of *Rhipiphorus* which we may fairly infer were not so occupied, for he would have recorded it had they been so: two he mentions having found solitary in worker-cells; and although he does not specify where or how he found the others engaged, still, if not in a cell with a wasp-grub, there is only one other place for them to be found in, viz. solitary in cells by themselves. Now I should like Mr. Smith to say what the mass of the larvæ are doing in cells by themselves. If it had been pupæ, we might have inferred that they had completed their task, eaten up their man, and retired from active life: but larvæ are different; they have still more or less of their task to do. Again, if Mr. Stone's observation is correct, we should never see any half-grown larvæ. There should be no medium between a "minute" one and a full-grown one, except during the forty-eight hours at which it is at its meal; but Mr. Smith speaks of specimens of under-grown larvæ; and if I am to suppose that the grubs I saw with a curd-like interior shining through the back were *Rhipiphorus*-grubs, then I can say for myself that I saw them of all sizes. In relation to this I may remark that Mr. Smith founds on the size of the perfect insect an argument which I am sure, on reconsideration, he will abandon. He argues that insects which in their larval state are dependent for their sustenance on chance or irregular supplies of food are apt to vary much in size, which is quite true; but he goes on to instance the *Rhipiphorus* as one of the examples of parasites that differ greatly in size. Now this, although true to the letter, is not true in

the spirit. The *Rhipiphorus* differs in size, but does not vary in size: this is not a distinction without a difference. There are two sizes; but these two are most constant. I have before me a series of about fifty of the smaller size taken out of the worker-cells, and they are as uniform in size as the workers of a hive of bees. The larger ones are scarce, but all I have seen are of one size, too, and they all come from the female cells. All the little ones come from worker-cells, all the big ones from queen-cells, just as in the case of the wasps themselves, where all the little wasps come from the worker-cells, all the big ones (the queens) from the queen-cells; and to me this fact is a strong confirmation of the view that they must both be fed in the same way, viz. by the wasps. Whether, as in the case of bees, the wasps feed the tenants of the queen-cells with any special food, or use any special treatment by means of which the grubs in the queen-cells are developed into queens and those in drone-cells into drones, I believe is not known; but the presumption is in its favour. If it were mere increase of size that was produced, it might be said that it was due to more food and more space in which to grow; but more food should not alter the sex. The *Rhipiphorus*, not being a wasp, would appear not to be affected by the same influence, so far as regards sex; for I have a male from a queen's cell, but only benefited by it in the increase of its size; and it may be merely the effect of a longer continuance of feeding and a greater supply of food, as supposed by Mr. Smith; but then he will surely not carry his argument to the extreme of supposing that the mere difference between eating a worker-grub and a queen-grub is sufficient to account for the greater dimensions of the one in a queen's cell over the one in a worker's cell.

But there are other and not less serious difficulties in the way of Mr. Smith's hypothesis. The *Rhipiphorus*-grub is described as attacking the wasp-grub at the head, "the mouth of the former buried in the body of the latter just below the head." Of course it must begin at the head: it could not begin at the tail, which is out of sight at the base of the cell; and equally, of course, it must eat its way inwards head foremost. When it has completed its repast, by which time it is to attain its full size, its position must therefore necessarily be head inmost, and it must perforce pass its metamorphosis in that position; for the cell is too narrow for it to turn in; and it cannot back out, for the entrance is closed by the lid. But what is the fact in nature? Putting aside the exceptional cases of doubtful position in cells doubly occupied, the *Rhipiphori* have invariably their head to the mouth of

the cell, exactly as the wasps, and fitting it as closely. This argument alone seems to me fatal to the hypothesis that the *Rhipiphorus*-larva limits itself to one victim.

The alternative hypothesis, by which it is supposed to feed on many, which I shall now consider, will be found to be no sounder. Supposing that the footless parasite larva roams about, emptying cell after cell, and clearing off wasp-grub after wasp-grub, and developing and increasing in the normal way at the expense of many, until the time approaches when it is to take its last meal and pass into the pupa state, it must by that time have attained considerable dimensions. A full-grown wasp-grub might indeed find room in its cell for a tiny *Rhipiphorus*-grub fresh out of the egg; but one about to pass into the pupa state, and nearly as big as itself, is another thing altogether. But might it not begin upon it with half or the whole of its body out of its victim's cell? No; because the cell has, by Mr. Smith's hypothesis, to be spun up by its victim; and it could not do this if the way were thus stopped, and, besides, it must not be so seriously injured or encroached on as to prevent its doing this. There is plainly no room to hold both. Two quarts of beer are not to be got into one quart bottle by any process hitherto found out. But Mr. Smith may abandon his lid-theory. He may admit the lid to be spun by the *Rhipiphorus*. But even then he has something else to get over. How is he to get the *Rhipiphorus*, which has entered the cell head foremost, turned round so as to have its head to the mouth of the cell? The creature, according to this theory, has the instinct of going head forward into the cells all the rest of its life. He must devise a new instinct for it to make it back out of the cell whose tenant it has eaten, and go on tail foremost into an empty cell when the proper time for it to back in comes. But if Mr. Smith admits all this—admits that the egg of the *Rhipiphorus* and of the wasp are the same and similarly placed, that the young larvæ of both are fed at first by the wasps, and that at last the mature larvæ of both spin the lids to their cells themselves—I think he must also admit that the whole of the abstract grounds on which the *Rhipiphorus* might be expected to have a different economy from that of the wasp is swept away. If it is admitted that it and the wasp do all the things that it seems unlikely they should do, there ceases to be any reason for denying that their economy is alike out and out, and that the same system of feeding by the wasps with which they commenced is continued to the end.

I shall now say a word or two as to Mr. Stone's observations: and here I may premise that, as will be evident to any

one who compares Mr. Smith's quotations from them and my brief allusion to them in my former paper, I had not Mr. Stone's paper before me when I wrote. My purpose then was to record my own observations, not to attack Mr. Stone's; and as I could not lay my hands on his paper, I rested satisfied with a quotation as to the nature of its contents, which I received from my friend Mr. Pascoe. But now that I have read it all, I see nothing, with the exception of the one case which I have already questioned, which appears to me incapable of explanation, or, when rightly interpreted, irreconcilable with the views I hold or with the observations I made. His interpretation is of course irreconcilable, but not the facts themselves.

Mr. Stone only gives two actual cases of the alleged attacks of the *Rhipiphorus*-larva on the wasp-grub. He infers more, and Mr. Smith infers more, from his finding, as he thinks, "these creatures retaining the skin and mandibles of their victim in their grasp even after they have passed into the pupa state." I shall speak to that immediately—one thing at a time; but as to actual cases of this attack, the two given by Mr. Stone are the only two recorded by him or by any other person whatever. Of part of the first I have already, to a certain extent, suggested an explanation; but a portion of it remains which is very difficult of explanation. He opens the sealed lid of a cell in which should be a pupa, finds in it a wasp-larva with a minute *Rhipiphorus*-larva attached to it with its mouth firmly buried in the body of its victim just below the head; and it appeared to have only very recently fastened on its victim. May it not be possible that, in handling the nest and picking out the larvæ from the cells, Mr. Stone had inadvertently dropped this minute *Rhipiphorus* from his forceps into either this newly opened cell or another beside it which he confounded with it? If it fell upon a larva, of course there is nothing to be surprised at in its eating it, as the wasp-grub would have done with it if it had got the first chance. Both are admitted to be carnivorous; and that they should eat each other when they have the opportunity is only what might be expected. That those which I found living amicably together, two in the same cell, did not attack each other, was no doubt due to their having been brought up together and sufficiently fed otherwise. They were like the members of a young family of lions, which, although ready enough to carry death and destruction with them out of doors, live in peace and harmony at home. The fact that the little *Rhipiphorus* had only commenced its attack is, I think, in favour of this supposition. It is against all the rules of pro-

bability that the cell should have been opened at that precise conjuncture of time that it began its attack. It is also still more unlikely that, having been sealed up with it, it should not have sooner made its attack. It is so disrespectful to the instinct of the *Rhipiphori* that the parent should have laid an egg in a cell already tenanted, and within reach of the jaws of the tenant, that I shall not suggest that alternative.

As to the *Rhipiphorus*-pupæ retaining the skin and mandibles of the grub they have eaten in their grasp, which Mr. Stone alleges of this one and of others which he subsequently observed, it is obviously a somewhat ludicrous blunder arising from a confusion of head and tail. I presume that by retaining in their grasp, he means holding in their jaws; they have no legs or claws to grasp with. But he must have forgotten that the parasite began at the head and, of course, finished off at the tail, and that it therefore should not be the mandibles that "it retained in its grasp," but the other end. But it seems to me clear that he had observed the old cast skin of the larva, which lies at the bottom of the cell, sticking to the tail of the pupa, not retained in its mouth. We know that the tail forms a powerful sucker; and, of course, it sucks up into its cup, like the bottom of a seaman's lead, anything that is lying loose at the bottom; and we know, too, that the last cast skin of a larva is very often found adhering to the chrysalis. We know, also, that when the larva undergoes its transformation, its muscles undergo a complete degradation, becoming like milk, and all muscular power on the part of the pupa at that particular period vanishes: As the change goes on, the muscular power is restored by the re-formation or consolidation of the muscles; but the idea of a pupa holding anything in its jaws by the tenacity of its muscular power seems to me an impossibility. I have only to add that none of my pupæ (and I have a number preserved in Canada balsam) has either skin or mandibles in its jaws, but most of them have them still adhering to the tail. This fact seems to prove that, like my pupæ, Mr. Stone's must have had their heads to the mouth of the cell, instead of in the position which his and Mr. Smith's hypothesis requires, at its base.

Next, as to the second and only other case of a *Rhipiphorus*-larva taken in the act of attacking a wasp-grub. The statement is as follows:—"I was fortunate in discovering a small larva of *Rhipiphorus* firmly attached to its victim; both were dead, and had become partially dried, so that, when immersed in spirits, they did not separate, but remained attached just as they were before death."

This seems to me to be a case of a double occupation of

one cell, similar to those which came under my notice; and the attachment of the one to the other is probably nothing more than what may be seen in every bottle of insects sent home from abroad or collected at home: some of the dying insects in their mortal agony have seized the nearest object with their mandibles, and arrive with a leg or some other part of their neighbour's body in their mouth, still firmly clasped in the death grip,—that is, supposing that the jaws of the one really are fastened in the body of the other. It may be only a mutual adhesion by lesion of the skin in the process of decay or drying up. I hope to see the specimen in Mr. Smith's hands before this goes to press; and if I do, and it contains any information, I will mention it in a postscript.

P.S. Since writing the above, I have seen the specimen in Mr. Smith's possession, and find it presenting almost exactly the same appearance as the specimen which I have above alluded to and which I have placed in the Collection of Economic Entomology in South-Kensington Museum. There are no means of saying whether the larvæ are merely in juxtaposition or if one has its jaws fastened on the other; but both are well grown, and except where they touch each other (where there is some lesion) they are uninjured. I have no doubt it is a case of double occupation of one cell, of the same nature as those described by me, and that, if the lesion (which I attribute to the pressure of the one upon the other) is not so great as to have destroyed the parts, Mr. Smith, on separating them, would find that they were not fastened to each other at all.

I had also the pleasure of showing to Mr. Smith my specimens of pupæ with the cast skin still sticking to their tail; and I think he will no longer regard Mr. Stone's observation of these cast skins as proof "of these creatures retaining the skin and mandibles of their victims in their grasp," nor as additional observed instances of the attack of the wasp-grub by *Rhipiphorus*-larvæ. As I stated at the outset, these observed instances are reduced, nominally, to two, but really only to one,—one of the two being that above mentioned, which I maintain is not an instance of attack at all, but of double occupation of cell; and the other, of actual devouring, which I have endeavoured to account for, but which, whether my explanation be the true one or not, is, I feel perfectly convinced, not to be regarded as a genuine normal example of the habits of the animal, but as arising from some error of observation.